



Female cognitive performance and mass are correlated with different aspects of mate choice in the zebra finch (*Taeniopygia guttata*)

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Abstract

A female's cognitive ability may influence her mate preferences through various mechanisms. These mechanisms include the direct effect of cognitive ability on the information-processing skills used during mate choice, and the indirect effect of cognitive ability on quality when females mate assortatively. Here, we examined whether the ability to learn a novel foraging task, a cognitive skill which has been associated with reproductive success in other capacities, was correlated with song preferences in female zebra finches (*Taeniopygia guttata*). Female preferences were measured in an operant testing chamber where hops on a perch triggered song playback. Females were given the choice of (1) conspecific vs. heterospecific song and (2) high-quality male vs. low-quality male conspecific song. We found that female performance on the novel foraging task was positively correlated with preference for conspecific song, but not with preference for high-quality male song. Instead, female mass was positively correlated with preference for high-quality male song, potentially signifying that female mass is a stronger predictor of female quality in assortative mating than female cognitive performance. Female mass and cognitive performance were unrelated. Our results suggest that the particular traits of a female that affect conspecific preference do not necessarily affect preference for high-quality males.

Keywords Sexual selection · Assortative mating · Cognitive ability · Conspecific preference · Female choice · Mate choice · Zebra finch · *Taeniopygia guttata*

Introduction

A female's choice of mate determines the genes and, in some species, the parental care that her offspring will receive (Andersson 1994; Jennions and Petrie 1997). Yet contrary to expectations, females do not uniformly prefer the same males (Jennions and Petrie 1997; Fawcett and Johnstone 2003; Holveck and Riebel 2010; Holveck et al.

2011). Instead, both conspecific preference and quality preference are affected by a number of extrinsic factors including availability of mates (Willis et al. 2011; Stoffer and Uetz 2015), costs of continued sampling (Johnson and Basolo 2003; Lynch et al. 2005; Byers et al. 2006), and social experience (Tudor and Morris 2009; Bailey 2011; Stoffer and Uetz 2015). Mate choice is also affected by the intrinsic factor of female quality (Bakker et al. 1999; Hunt et al. 2005; Burley and Foster 2006; Holveck and Riebel 2010; Griggio and Hoi 2010; Holveck et al. 2011). When a female is of high quality and the costs of being choosy are low, she is likely to devote ample resources to finding a high-quality male. When she is of lower quality and/or the costs of being choosy are higher, she may devote fewer resources to sampling males and be willing to accept a lower quality male (Fawcett and Johnstone 2003; Härdling and Kokko 2005; Burley and Foster 2006). In some instances, she may even be willing to accept a heterospecific male, leading to hybridization (Nuechterlein and Buitron 1998; Pfennig 2007; Willis et al. 2011). There is also evidence that low-quality females sometimes actively

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prefer males that match their own quality and engage in assortative mating (Basolo 2004; Bel-Venner et al. 2008; Holveck and Riebel 2010; Griggio and Hoi 2010; Holveck et al. 2011). This is distinct from simply reducing choosiness; in this case, females assortatively mate based on quality.

A female's cognitive ability may affect her mate choice decisions by affecting her quality in assortative mating. By "quality", we refer to female fecundity and the ability to provide resources for her offspring, factors that are often gauged via body condition and factors that affect body condition, such as maternal brood size (Tsichirren et al. 2009; Holveck et al. 2011). In addition to body condition, there is also evidence that cognitive ability can impact fecundity and ability to provide resources for her offspring. A study of population decline in kittiwakes (*Rissa brevirostris*) found that nutritional factors that negatively impact problem-solving ability also negatively impact population growth (Kitaysky et al. 2006). Recent studies in the wild with great tits (*Parus major*, Cole et al. 2012; Cauchard et al. 2013) and Australian magpies (*Cracticus tibicen dorsalis*, Ashton et al. 2018) suggest that cognitive skills also affect the degree to which a female is able to utilize resources in her territory to provide for herself and her offspring. Thus, better cognitive skills may positively increase a female's fecundity and ability to provide resources for offspring, and thereby affect mate choice decisions when females mate assortatively based on quality.

Cognitive ability may also impact mate choice by affecting the degree to which a female can process information. Processing extrinsic (e.g., a potential mate's traits) and intrinsic (e.g., a female's own quality) factors in the context of a mating decision is a cognitively demanding task that can utilize some of the same heuristics humans use when making comparative evaluations (Bateson and Healy 2005; Corral-López et al. 2017; Burley et al. 2018). Many males advertise themselves via multiple signals (Searcy and Nowicki 2005) that females must assess and compare (Andersson 1994; Bateson and Healy 2005; Burley et al. 2018). The cognitively demanding nature of mate choice is especially true in species with sexual signals such as bird song, which is learned by both males and females during a sensitive period of development (Catchpole and Slater 2008). While males learn to produce songs, females also learn to recognize and even generalize songs of familiar males, later showing a preference for local dialects even within the same species (Clayton 1990a; Anderson et al. 2014; Holveck and Riebel 2014). Female songbird mating decisions thus depend on learning, memory, and comparative evaluation processes that take into account prior experiences and currently available mating options. Despite the role that information processing plays in mate choice, there has been little investigation into whether performance on a different cognitive task is

correlated with a female's mating signal preferences or mate choice decisions (Bateson and Healy 2005).

In this experiment, we tested whether variation in female zebra finch (*Taeniopygia guttata*) cognitive performance was correlated with strength of preference using two contrasts: conspecific song versus heterospecific song and high-quality song versus low-quality song.

There is evidence that cognition in birds is modular, rather than general (reviewed in Searcy and Nowicki 2019), meaning that the neural circuits required for performing different tasks are largely independent and self-contained (Shettleworth 2012). However, we do not necessarily know which cognitive abilities are associated, and whether there are underlying traits (e.g., personality or sensory processing) that affect multiple cognitive abilities. When determining which cognitive task was of most interest, we therefore chose to use a novel foraging task, because performance on foraging-related problem-solving tasks (i.e., removing an obstacle to get to a reward) has been correlated with fitness consequences in the wild (Cole et al. 2012; Cauchard et al. 2013), and because performance on foraging tasks influences female mate choice when observed directly in males (Chantal et al. 2016; Chen et al. 2019). In this way, we were looking at a cognitive ability that was known to influence reproductive success in birds and asking how it was correlated with mate choice decisions. We expected that performance on this fitness-related task would be positively correlated with performance on another fitness-related task, selecting the best possible mate. We expected these both because zebra finches have been known to engage in assortative mating and better learners of a foraging task are theoretically of better quality, and because there may be underlying cognitive and personality traits that affect both tasks. We therefore predicted that female performance on the novel foraging task would be positively correlated with preferences for songs that reflected the higher fitness choice: conspecific song, in the case of conspecific vs. heterospecific song, and high-quality song, in the case of high-quality vs. low-quality song.

Methods

Subjects and housing

48 adult zebra finches, 25 males and 23 females, of unspecified age and lineage were obtained from Magnolia Farms avian breeder. All birds were housed for 4 days in a group cage upon arrival, and then placed in individual or single-sex pair cages. Males and females were massed using a Pesola spring scale just prior to being placed in individual cages. Cages were made of wire and measured 48 cm × 25 cm × 30 cm. Each cage contained two perches,

one cuttlebone, and food and water provided ad libitum. Rooms were illuminated on a 12 h:12 h light–dark cycle and temperature was maintained at 22 °C. Males and females were housed together. Housing conditions approved by Tulane IACUC Protocol 0427R.

Cognition assay

In the novel foraging task, birds learned to remove lids covering wells to obtain a food reward (the motor portion) and to associate lids of a certain color with the food reward (the color association portion; see Boogert et al. 2008, 2011; Anderson et al. 2017; DuBois et al. 2018). All males and females were tested. The number of trials it took to complete both portions of the novel foraging task was totaled for a measure of speed to learn, and scores on individual motor and color association portions were also recorded, as there is speculation that these portions of the task represent different cognitive skills (Audet and Lefebvre 2017). Birds were tested in the housing room and remained in auditory contact with neighbors to reduce stress caused by social isolation. However, dividers were placed between cages, so that neighbors could not see the task before they were tested.

In the motor portion of the task, birds learned to remove lids that covered wells drilled into a 10×14 cm gray composite block. Lids were a mixture of blue and yellow and fitted snugly into the wells (1.7 cm diameter, 1 cm depth), so that they could not be accidentally kicked or brushed off the wells, but had to be pried off. Each block had six wells, four of which were covered and baited with two to three millet seeds on any given trial. The motor portion of the task was broken down into five steps: (1) foraging grid with food but no lids, (2) lid next to well, (3) lid half-covering well, (4) lid tipped into well, and (5) lid fully covering each well. Birds were given six trials per day, and each trial consisted of a 2-min period in which the block was placed in the cage and birds were allowed to interact with it. The researcher conducting the trial was hidden to reduce stress for the bird. Birds had to eat from at least two wells to pass a trial, and had to pass three out of four consecutive trials to pass a step.

The color association portion of the task followed the motor portion, as birds had to learn to remove lids before learning to associate lid color with a reward. In this portion of the task, two blocks were used, but only wells with one of the lid colors were baited (either blue or yellow). Color was randomly assigned to each bird at the start of the task. To pass a color association trial, birds had to remove all lids of the rewarded color before attempting to remove lids of the unrewarded color. To pass the color association portion of the task, birds had to pass six out of seven trials in a row (i.e., they could pass five trials, fail one, and pass one more in order to pass the task). Birds were given six trials a day, with 10-min intervals between

trials, 5 days a week. Food was removed 5 h before testing for both motor and color association trials to motivate birds. Motivation checks, in which food was placed back into the cage, were done after each session. Birds were considered motivated if they approached food within 1 min and not motivated if they did not. All birds passed all motivation tests.

If a bird did not pass a particular stage after testing for more than 4 days (i.e., > 24 trials), it was moved back to a previous stage or, for the initial stage only, the block was left in the cage overnight to habituate the bird to its presence. If a bird did not pass a particular stage after testing for more than 60 trials, the bird was removed from further testing and designated a non-solver.

Song recording and stimulus sets

Male song was recorded in sound isolation chambers (Industrial Acoustics) with Shure SM57 directional microphones. To evoke directed song (ten Cate 1985), males were placed in divided cages with a randomly selected female in the other half. The pair was placed in the chamber and allowed to acclimate for 24 h before recording began. Recording took place during the subsequent 24 h, during which time typical males produced hundreds of songs.

Four conspecific vs. heterospecific and six high-quality vs. low-quality stimulus sets were created to test female preference. To create stimulus sets, males were classified based on their cognitive performance and mass. Males were initially designated high-quality or low-quality based on whether they were able to solve the novel foraging task. High-quality males were the six fastest males to solve the task (mean = 41.5 trials, s.d. = 10.0), while low-quality males were six males unable to solve the task (mean = 90.7 trials, s.d. = 19.4 before pulled from testing). High-quality males were also significantly heavier as determined by a *t* test than low-quality males (high-quality mass mean = 14.68 g, low-quality mass mean = 12.80 g, *t* = 2.804, *df* = 8.7, *p* value = 0.021). This was done to maximize the disparity between high-quality and low-quality males in cognitive performance, and because solver/non-solver differences have been associated with fitness differences in the wild (Cole et al. 2012; Cauchard et al. 2013). To create conspecific stimuli used in the conspecific vs. heterospecific trials, songs from average performers (mean = 97 trials) were recorded and paired with songs from rufous-collared sparrows (*Zonotrichia capensis*). The longest song was selected from each male to provide females with the best performance from his repertoire, as females generally prefer longer and more complex song (Riebel 2009a). See Online Resource 1 for information regarding stimulus song length and complexity.

Song preference assay

We used an operant protocol modeled after Anderson et al. (2014). Prior to assay, female cages were moved into a sound attenuation chamber and females were given 24 h to habituate. After habituation, cages were equipped with two operant perches on the front of the cage positioned approximately 10 cm high and 25 cm apart, in addition to the two normal perches that were placed diagonally between the back and each side of the cage. Each experimental perch was 9 cm long and had a $\frac{1}{2}$ cm diameter. Perches were made of wood and attached to micro-switches (Honeywell), such that when a bird landed on the perch, it lowered slightly and triggered playback of a particular song through a speaker. Songs were played at 65 dB SPL from the center of the chamber, and counts of hops and playbacks were collected through Sound Analysis Pro (see Tchernichovski et al. 2000). Food and water were provided ad libitum in the operant chambers.

Females were first presented with conspecific vs. heterospecific songs for 2 days. On the first day, conspecific song was randomly assigned to either the right or left perch and heterospecific song to the other. On the second day, conspecific and heterospecific song switched sides, to control for side bias. Trials ran from 11 am to 5 pm each day, during which time the hops on each perch were recorded, and outside of which, hops did not trigger playback of song. The initial conspecific vs. heterospecific assay also served as the learning period for the operant preference assay. To ensure that females had learned to trigger song playback by hopping on the operant perches, trials were not counted unless a female hopped on both perches at least once, and females did not move on to the high-quality vs. low-quality trials until they had hopped on both perches for 2 days in a row, giving 2 days of conspecific vs. heterospecific preference data.

Females were next presented with high-quality song vs. low-quality song. Each female was tested four times, for a total of four trials. To limit the potentially confounding effects of a stimulus song that was particularly attractive or unattractive to an individual, females were presented with multiple stimulus sets and responses to multiple sets were aggregated. Each female heard four of six possible stimulus sets, again with sides of a particular stimulus type being switched each day to control for side bias.

Statistical analyses

To account for differing levels of activity among females and side bias, song preference was calculated as the number of hops triggering the expected preferred song divided by the total number of hops during that song type trial (see Anderson et al. 2014). Thus, in the conspecific vs. heterospecific assay, we calculated number of conspecific hops divided by the sum of conspecific and heterospecific hops; in the

high-quality vs. low-quality assay, we calculated number of high-quality hops divided by the sum of high-quality and low-quality hops. We also calculated the average number of hops per trial to determine whether hop activity was correlated with strength of preference.

We ran linear models in *R* (*R* Development Core Team 2016) using the total preference data (total conspecific hops divided by the sum of conspecific and heterospecific hops, and total high-quality hops divided by the sum of high-quality and low-quality hops), cognitive score (number of trials to solve the task) including scores on separate stages, activity level (total hops), and female mass. We also wanted to test whether stimulus set, testing day, or female ID had an effect on female preference. To do this, we separated female preferences by day and ran mixed effect linear models on all data, using cognitive score, activity level, and female mass as fixed effects and testing day, stimulus set, and female ID as random effects. Mixed effect linear models were also performed in *R*, using the package lme4 (Bates et al. 2015). Models were then compared using Akaike's information criterion (AIC).

For both the conspecific vs. heterospecific and high-quality vs. low-quality preference assay, we compared conspecific and high-quality preference to the null (0.5 preference; i.e., birds randomly hopping between both perches) using a one-sample *t* test.

Results

Cognitive assay results

23 females and 25 males were tested with the cognition assay. Of these, 6 females and 7 males did not pass a given stage within 60 trials and were pulled from testing. Of the birds that passed, females took an average of 35.41 trials (s.d. = 17.01) to pass the motor stage and 26.10 trials (s.d. = 14.83) to pass the color association stage, with a total of 61.47 (s.d. = 26.10) trials to pass the novel foraging task (motor + color association). Males took an average of 43.61 (s.d. = 22.40) trials to pass the motor stage and 19.78 (s.d. = 8.63) trials to pass the color association stage, with a total of 63.39 (s.d. = 25.06) trials to pass the novel foraging task. Individual performances on the motor and the color association tasks were not correlated in females (Multiple *R*-squared = 0.114, Adjusted *R*-squared = 0.050, *F*-statistic = 1.796 on 1 and 14 *df*, *p* value = 0.202; see Online Resource 2) or males (Multiple *R*-squared = 0.018, Adjusted *R*-squared = -0.044, *F*-statistic = 0.290 on 1 and 16 *df*, *p* value = 0.598; see Online Resource 2). Within learners, there was no correlation between mass and overall learning score in females ($t = 0.516$, $df = 14$, *p* value = 0.614) or males ($t = 0.501$, $df = 16$, *p* value = 0.623). However, among

males, non-solvers were significantly lighter than solvers ($t = -4.239$, $df = 18.62$, p value = 0.000462). This pattern did not hold among females ($t = -0.323$, $df = 18.67$, p value = 0.751). There was a significant, but weak correlation between how quickly a bird solved the first step of the motor task and how quickly it solved the total task (Multiple R -squared = 0.146, Adjusted R -squared = 0.119, F -statistic = 5.465 on 1 and 32 df , p value = 0.026). Because speed to approach a novel object is often used as a proxy for neophobia (Bouchard et al. 2007; Cauchard et al. 2013; Shaw et al. 2015), this may indicate that aspects of temperament, such as boldness, were correlated with overall learning score (Rowe and Healy 2014).

Females generally preferred conspecific but not high-quality male song

Nineteen females were tested in the operant assay. Females significantly preferred conspecific song (one-sample t test compared to null 0.5, $t = 5.945$, $df = 18$, p value = 0.0000126). There was not a group-wide preference for the songs of high-quality males (One-sample t test compared to null 0.5, $t = 1.480$, $df = 18$, p value = 0.156).

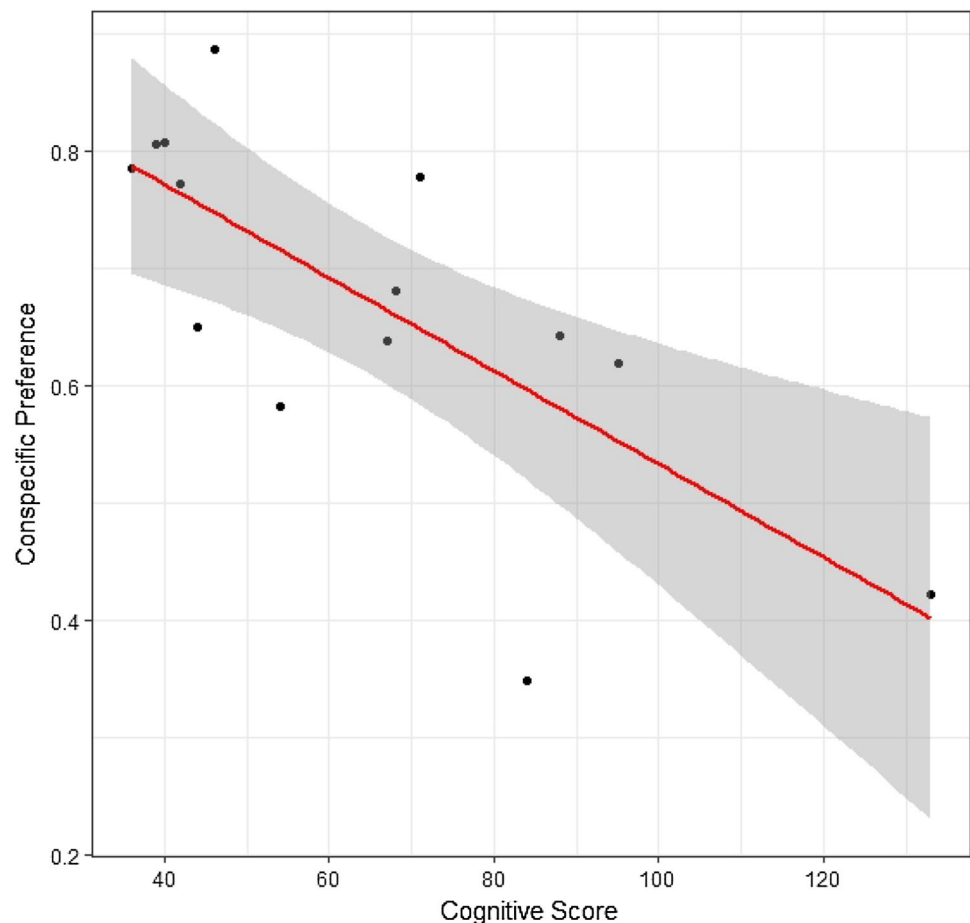
Some individuals preferred the songs of high-quality males, whereas others preferred the songs of low-quality males, resulting in a net preference that did not differ from the null.

Cognitive ability predicted conspecific preference, but not high-quality preference

Females that performed better on the novel foraging task had stronger preferences for conspecific song (see Fig. 1; Multiple R -squared = 0.5342, Adjusted R -squared = 0.4954, F -statistic = 13.76 on 1 and 12 df , p value = 0.002983) even when two females that did not prefer conspecific song were dropped from the analysis (Multiple R -squared: 0.3449, Adjusted R -squared: 0.2794, F -statistic: 5.264 on 1 and 10 DF , p value: 0.04468). Non-solvers ($n = 5$) were not included in this analysis, because they did not have a score on the assay, and because reasons for being a non-solver may include factors beyond cognitive ability (Rowe and Healy 2014).

When analyzed separately, scores on both the motor (Multiple R -squared = 0.387, Adjusted R -squared = 0.336, F -statistic = 7.58 on 1 and 12 df , p value = 0.017) and color association (Multiple R -squared = 0.305, Adjusted

Fig. 1 Females that performed better on the novel foraging task had stronger preferences for conspecific song. The total number of trials for a female to complete the novel foraging task had an inverse relationship with conspecific preference, such that females who solved the task in the fewest number of trials had the largest preference ratio for conspecific song (Multiple R -squared = 0.534, Adjusted R -squared = 0.495, F -statistic = 13.76 on 1 and 12 df , p value = 0.00298). Red line represents linear model; gray margins indicate 95% confidence interval



R -squared = 0.247, F -statistic = 5.261 on 1 and 12 df , p value = 0.041) portion of the task were inversely correlated with conspecific preference, such that faster learners on each portion of the task had stronger conspecific preferences. However, there was no significant relationship between scores on motor performance and on color association in the females that went through preference assays (Multiple R -squared = 0.09883, Adjusted R -squared = 0.02373, F -statistic = 1.316 on 1 and 12 df , p value = 0.2737).

Score on the novel foraging task did not predict female preference for the songs of high-quality males (Multiple R -squared = 0.031, Adjusted R -squared = -0.058, F -statistic = 0.347 on 1 and 11 df , p value = 0.568). Furthermore, preference for conspecific song was not correlated with preference for high-quality song (Multiple R -squared = 0.004, Adjusted R -squared = -0.059, F -statistic = 0.004 on 1 and 17 df , p value = 0.951; see Online Resource 3).

Mass predicted high-quality preference, but not conspecific preference

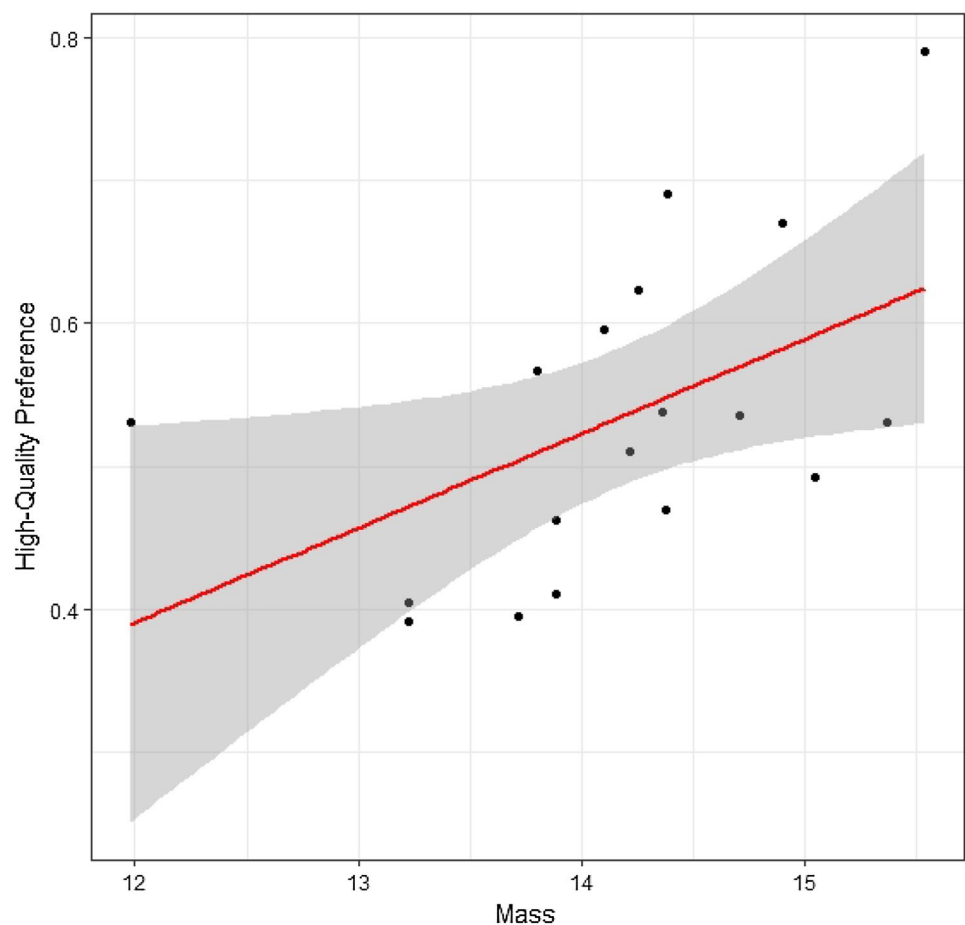
Female mass did not predict conspecific preference (Multiple R -squared = 0.00239, Adjusted R -squared = -0.056,

F -statistic = 0.038 on 1 and 16 df , p value = 0.847). However, heavier females preferred high-quality males (see Fig. 2; Multiple R -squared = 0.259, Adjusted R -squared = 0.212, F -statistic = 5.583 on 1 and 16 df , p value = 0.0311). Female mass was not correlated with score on the novel foraging task (Multiple R -squared = 0.00845, Adjusted R -squared = 0.0165, F -statistic = 1.201 on 1 and 11 df , p value = 0.297). Non-solver females were included in mass analyses, but one female's mass measurements were not available, and thus, our sample size was 18.

Activity level was not correlated with other metrics

The average number of hops per day was not correlated with conspecific preference (Multiple R -squared = 0.061, Adjusted R -squared = 0.014, F -statistic = 1.263 on 1 and 17 df , p value = 0.277), high-quality preference (Multiple R -squared = 0.003, Adjusted R -squared = -0.056, F -statistic = 0.472 on 1 and 17 df , p value = 0.831), score on the novel foraging task (Multiple R -squared = 0.052, Adjusted R -squared = -0.027, F -statistic = 0.653 on 1 and 12 df , p value = 0.435), or mass (Multiple R -squared = 0.004,

Fig. 2 Heavier females preferred high-quality males and lighter females preferred low-quality males (Multiple R -squared = 0.259, Adjusted R -squared = 0.212, F -statistic = 5.583 on 1 and 16 df , p value = 0.0311). Red line represents linear model; gray margins indicate 95% confidence interval



Adjusted R -squared = -0.058 , F -statistic = 0.061 on 1 and 16 df , p value = 0.809).

Stimulus set and testing day did not affect preferences

We also ran mixed effects linear models using hop data from each individual testing day to include stimulus set, testing day, and female ID as random effects. Models that included only fixed effects (i.e., learning score for conspecific preference and mass for high-quality preference) were more informative than models that also included single and multiple random effects. Thus, information about stimulus set, testing day, or female ID does not improve model fit to female preference data (see Online Resource 4 for AIC values).

Discussion

There are two significant results from our experiment: females that were faster to solve a novel foraging task showed stronger preferences for conspecific over heterospecific song, and heavier females showed stronger preferences for the songs of high-quality males whereas lighter females showed stronger preferences for low-quality males. Our prediction that females that scored better on the novel foraging task would have stronger conspecific preferences was supported. Our prediction that females that scored better on the task would have stronger preferences for high quality male song was not supported; instead, we found that female mass strongly predicted preference for high- and low-quality songs.

These findings are consistent with studies that have examined the effects of developmental stress on mate choice. Developmental stress has been shown to affect a number of cognitive processes in birds and other animals, including spatial memory (Pravosudov et al. 2005), auditory learning (Farrell et al. 2016), song production (Nowicki et al. 2002; Buchanan et al. 2003), and associative learning (Kitaysky et al. 2006). The effects of developmental stress on mating preferences have been tested in three oscine species: song sparrows (*Melospiza melodia*, Schmidt et al. 2013), zebra finches (*Taeniopygia guttata*, Woodgate et al. 2011; Sewall et al. 2018), and European starlings (*Sturnus vulgaris*, Farrell et al. 2015). Two of these studies (Schmidt et al. 2013; Farrell et al. 2015) tested conspecific preference followed by a test of preference for some aspect of song quality, and both found that conspecific preference was reduced by developmental stress, but that preference for intraspecific song variation (e.g., preference for longer songs in Farrell et al. 2015 and high-complexity songs in Schmidt et al. 2013) was not. Preference for high-complexity song was also not affected

by developmental stress in Woodgate et al. 2011, though this was not contrasted with conspecific preference. The deleterious cognitive effects of developmental stress thus appear to affect conspecific preference but not quality preference, consistent with our findings in which cognitive performance was positively correlated with conspecific preference but not quality preference.

In interpreting our results, both alone and in conjunction with the previous developmental stress studies, we must consider the possibility that our measure of learning ability on the novel foraging task predicted a female's ability to learn the operant set-up rather than the strength of her conspecific preference. In our study, conspecific preference was tested first. Females with poorer learning ability may have been slower to learn the operant assay and thus did not learn to associate a particular perch with a preferred song until later trials. However, three of the developmental stress experiments (Schmidt et al. 2013; Farrell et al. 2015; Sewall et al. 2018) also found that the neural response for conspecific song, as measured by immediate-early gene expression, was reduced by developmental stress. This indicates that a reduction in conspecific preference is not solely due to problems associated with learning the experimental apparatus, but that there are differences in response to conspecific song at the neural level which impact the expression of preferences.

The finding that female mass was correlated with preference for high-quality male song is also consistent with previous research that found assortative mating based on brood size in zebra finches (Holveck and Riebel 2010; Holveck et al. 2011). Brood size inversely affects body mass among other aspects of body condition, and females from larger broods have been found to prefer males from large broods even when given the choice of a male from a small brood (Holveck and Riebel 2010). Our findings did not support the original prediction that females that performed better on a novel foraging task would select songs from higher quality males. Our findings instead suggest that when aspects of female quality are not correlated (here, mass and cognitive performance), mass may be the best predictor of female preference. We are not able to tease apart whether heavier females were selecting high-quality song because those songs were produced by males with greater cognitive ability or because those songs were produced by heavier males, because stimuli were drawn from males that both scored better on the task and had higher body masses.

We tested mate choice using males and females that had been housed with each other, rather than naïve females, because we wanted to mimic natural flock conditions. In the wild, zebra finches are flock birds and females often select mates from among familiar males (Zann 1996). One benefit of this approach, besides testing for mating preferences in a more biologically relevant context, is that we avoided making assumptions about which sexual signal (e.g., beak

color or song) females use to make decisions (Riebel 2009b). Because males were familiar, song served as a cue to male identity and was not the only information available. Using familiar males with unknown lineages does open the possibility that females would be biased toward the song of their father or foster father, a preference which has been shown in zebra finches (Clayton 1990b). However, we tested females on multiple stimulus pairs, reducing the effect that any one particularly attractive stimulus song would have on female preference. Our analyses also found that a given stimulus set did not predict variation in female preference, further suggesting that females were not biased towards a particular song. Repeating this experiment using the stimuli of unfamiliar males would provide a useful comparison in the future to understand the role of familiarity in explaining preferences.

The extent to which artificial tasks (such as our novel foraging task) can be used to measure cognitive ability, and the extent to which performance on those tasks is altered by personality or motivation, has been greatly debated among animal behaviorists (Griffin and Guez 2014; Rowe and Healy 2014; Griffin et al. 2015; Dougherty and Guillelte 2018). We chose to dichotomously categorize males into fast solvers (mean = 41.5 trials to solve) and non-solvers (mean = 90.7 trials before pulled from testing) because similar binomial categorizations have been associated with fitness consequences in the wild (Cole et al. 2012; Cauchard et al. 2013). In males, we were interested in overall quality, not in determining which variables were contributing to quality. Therefore, we used non-solvers as our low-quality males, because regardless of whether cognitive ability or personality had the strongest effect on male cognitive performance, it is reasonable to assume that fitness consequences are associated performance on learning tasks. Furthermore, females have shown preferences for males they observed solving a foraging task (Snowberg and Benkman 2009; Chantal et al. 2016; Chen et al. 2019), indicating that better foragers are more desirable mates. In addition, stimulus males who quickly solved the task were heavier than non-solvers, which increased our confidence that we separated males based on biologically relevant factors. However, definitively sorting males based on quality is difficult to do without experimentally manipulating their condition. In females, we excluded non-solvers in our analysis of learning ability, because we wanted to test how differences in ability to do the same task mapped onto preference. Non-solvers were categorically different in ability.

One interesting facet of our results is the finding that conspecific preference and quality preference were most strongly affected by different aspects of the female. Recent literature has contended that selection of conspecific males (“species recognition”) is not distinct from selection for high-quality males, as there is one axis of quality that

ranges from an incompatible heterospecific mate to a high-quality, high-compatibility conspecific mate (Snowberg and Benkman 2009; Mendelson and Shaw 2012). While not directly contradicting this hypothesis, our results suggest that the relationship between conspecific preference and high-quality preference may be more complicated, as cognitive performance more strongly affects the categorical choice between conspecific and heterospecific song than the choice between two different conspecific songs of differing quality (also supported by Woodgate et al. 2011; Schmidt et al. 2013; Farrell et al. 2015). It is possible that females are using the same neural process to assess conspecific vs. heterospecific song and high-quality vs low-quality song, as Mendelson and Shaw (2012) and Snowberg and Benkman (2009) predict. However, our results suggest that it is also possible that like many aspects of neural encoding of song (e.g., Prather et al. 2009), discerning between conspecific vs. heterospecific song is a categorical decision and governed by a different neural process than mate choice among conspecifics, which is a continuous assessment of quality vs. available resources (Jennions and Petrie 1997). Future work examining the neural mechanisms behind conspecific preference and mate-quality preference may provide insight.

Our results indicate that while a measure of cognitive ability may play a role in assessing and responding to conspecific song, other factors contribute to acquiring a high-quality mate, and a female that responds more strongly to conspecific song will not necessarily respond more strongly to high-quality song. Instead, there may be a complex relationship between cognitive ability, female quality, and mate choice decisions. Future study of the neural mechanisms behind conspecific vs. quality preference could not only add to the discussion on species recognition (Mendelson and Shaw 2012), but also add to our general knowledge of how environmental factors that limit cognitive ability, such as diet changes (Kitaysky et al. 2006) and developmental stress (Pravosudov et al. 2005; Fisher et al. 2006; Kriengwatana et al. 2015), can impact mate choice decisions in females.

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Data availability Data available on Dryad.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All procedures performed in studies involving animals were in accordance with the ethical standards of the Tulane Animal Care and Use Committee, Protocol 0427R.

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